ANALYZING NEURAL, BEHAVIORAL, AND EMG DATA FROM MONKEYS DURING MOVING AND HOLDING

by
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Abstract

Some neuroscientists posit that motor control is the sole reason for the existence of a complex nervous system. This is evidenced by the action of sea squirts that consume their own brain as soon as they do not require any further locomotion in life. By this reasoning, other functions of the brain are evolved to predict movements in the future so as to drive or suppress them. This work analyzes two different aspects of the motor system - its ability to encode position, movement, and state of action and its role in short-term memory of movements.

In this thesis, Chapter 2 looks for evidence for the presence of a neural integrator involved in finger movements. On analyzing four different types of finger movements, a high correlation is observed between the mean muscle activity during the hold period and the integral of the muscle activity during the preceding move period. This suggests the presence of a neural integrator for finger movements, that is involved integrating the move commands to encode position. Chapter 3 analyzes how four different areas of the brain (the primary motor cortex, the reticular formation, the spinal cord, and the deep cerebellar nuclei) encode movement, position, and state. The second part of this analysis looks for how the position is encoded by all the four areas of the brain.

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Acknowledgments

I thank my advisor Dr. Reza Shadmehr for the continued support and guidance in my master's research. I am immensely grateful to Dr. Scott Albert, my mentor, for the invaluable advice and insights throughout the project. Also, this project would not have been possible without the data from Dr. Stuart Baker's lab in the New Castle University, United Kingdom. I thank Dr. Stuart Baker and Dr. Demetris Soteropoulos for sharing the data. I would also like to thank the members of the thesis committee for their support in this thesis.

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Introduction

1.1 The experiment

The data for the analysis was recorded by Dr. Stuart Baker and Dr. Demetris Soteropoulos at the Newcastle University, UK[9].

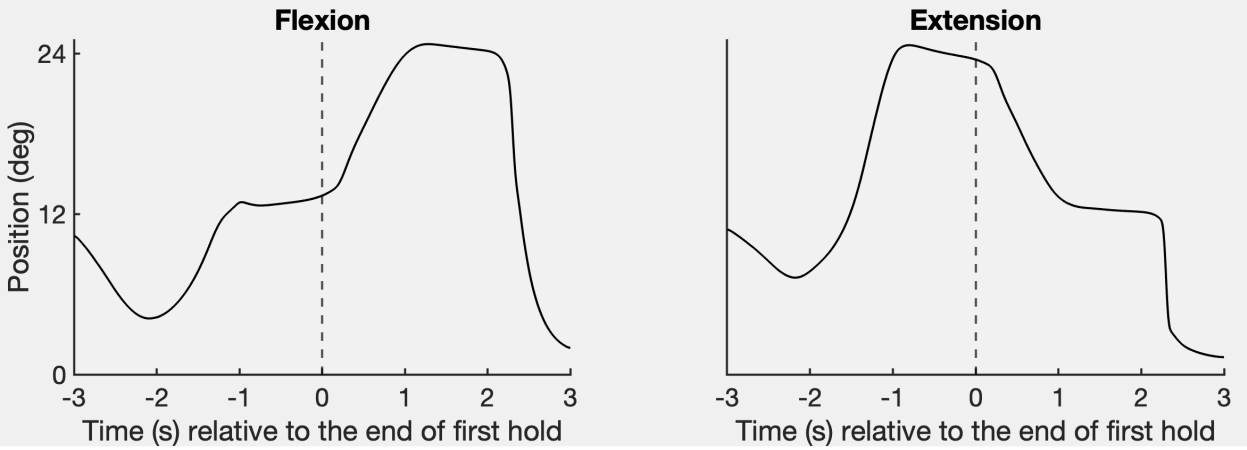


Figure 1.1: The mean position of the flexion and extension movements across all the sessions

The data were collected from two monkeys. Each of them were seated on a chair, and each one of them was visually presented with a target on the screen. The task was was to

trace the movement of the target using the index finger. The movement was restricted to the metacarpophalangeal joint of this finger. The experiment was set up in such a way as to allow the finger to execute two types of movements - flexion and extension (figure 1.1). For a trial with the flexion movement, the target appears at the position 12^o, remains stationary for a second (the first hold period), and moves to the position 24^o with a velocity $12^o/s$ for one second (the move period), and is held at 24^o for a second (the second hold period). On the other hand, for trials with extension movement, the target appears at the position 24^o, remains stationary for a second (the first hold period), and moves to the position 12^o with a velocity $12^o/s$ for one second (the move period), and is held at 12^o for a second (the second hold period). The neural, EMG, and position data for all of these trials were recorded.

The EMG data were recorded from the first dorsal interosseous (1DI) muscle, the extensor digitorum communis (EDC) muscle, the flexor digitorum superficialis (FDS) muscle, the flexor digitorum profundus (FDP) muscle, the flexor carpi radialis (FCR) muscle, the extensor carpi

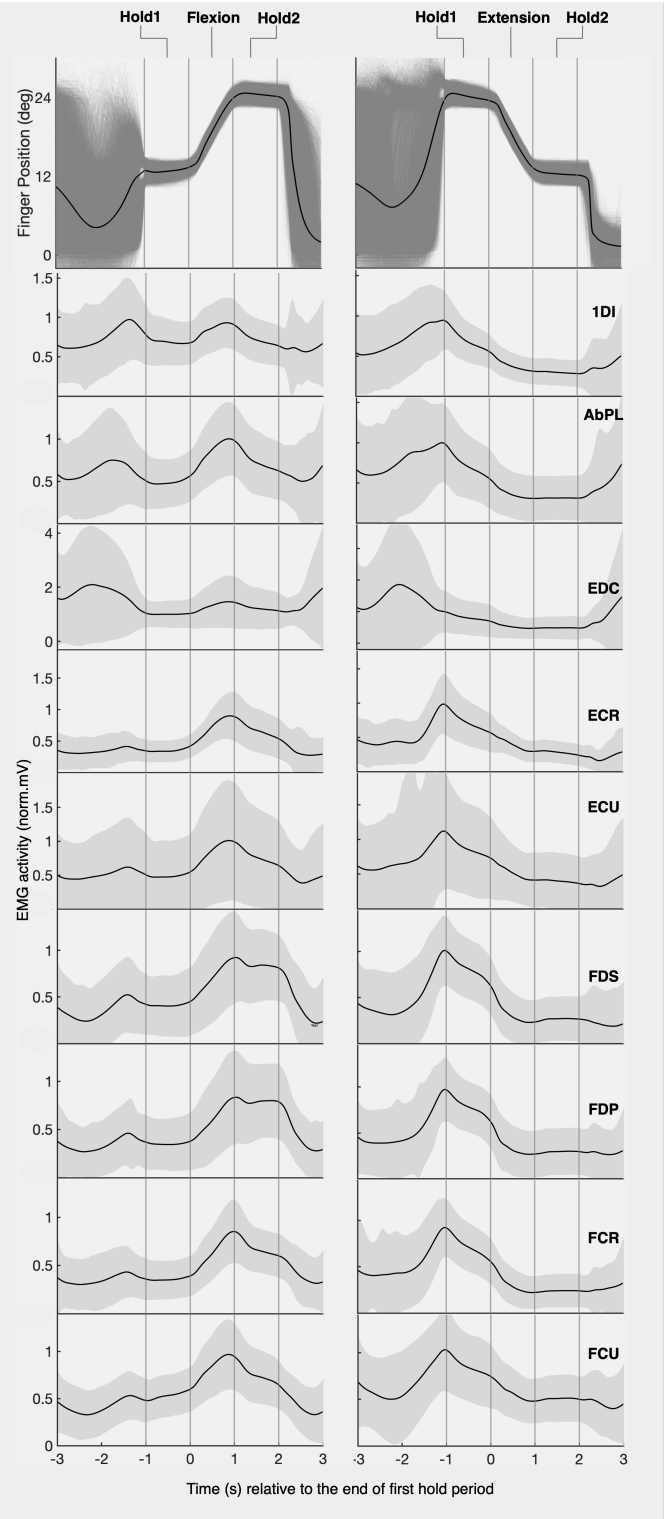


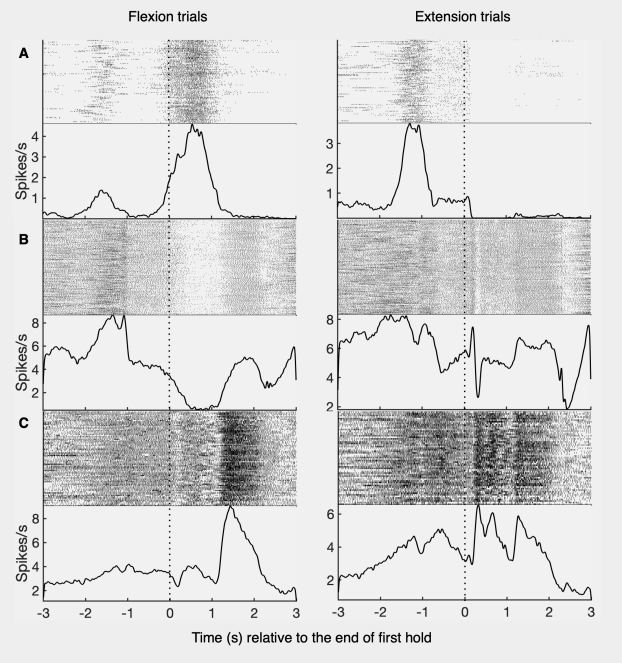
Figure 1.2: The mean EMG activity of all nine muscles for flexion and extension

ulnaris (ECU) muscle, the abductor pollicis longus (AbPL) muscle, the extensor carpi radialis (ECR) muscle, and the flexor carpi ulnaris (FCU) muscle. There were 191 sessions of recordings in total. The mean activity of these muscles during flexion and extension movements are shown for all the sessions is given in figure 1.2.

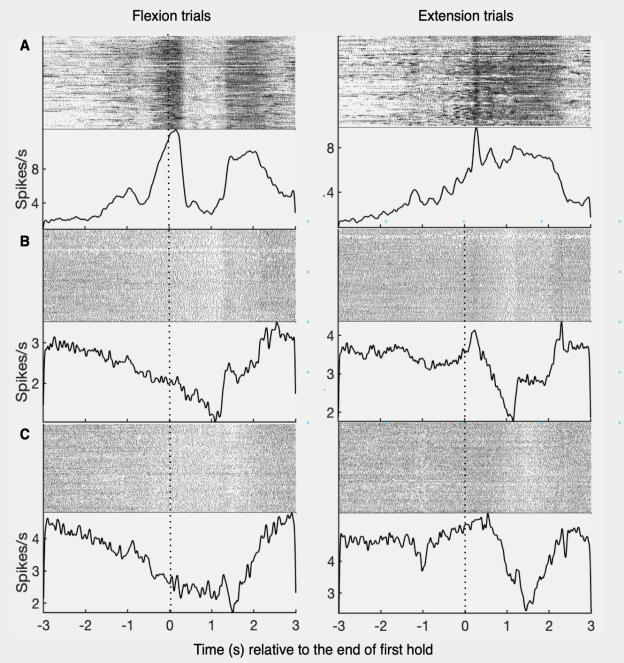
The neural data were recorded from four different brain regions - the primary motor cortex, the reticular formation, the spinal cord, and the deep cerebellar nuclei. The recordings were taken from a total of 585 neurons. The raster plots and peristimulus time histograms of some example neurons from the primary motor cortex are shown in figure 1.3a, those from deep cerebellar nuclei are shown in figure 1.3d, those from spinal cord are shown in figure 1.3c, and those from reticular formation are shown in figure 1.3b. The position trace for the two types of movements are shown in figure 1.1. All data are aligned to the start of the movement.

1.2 The two studies on the data

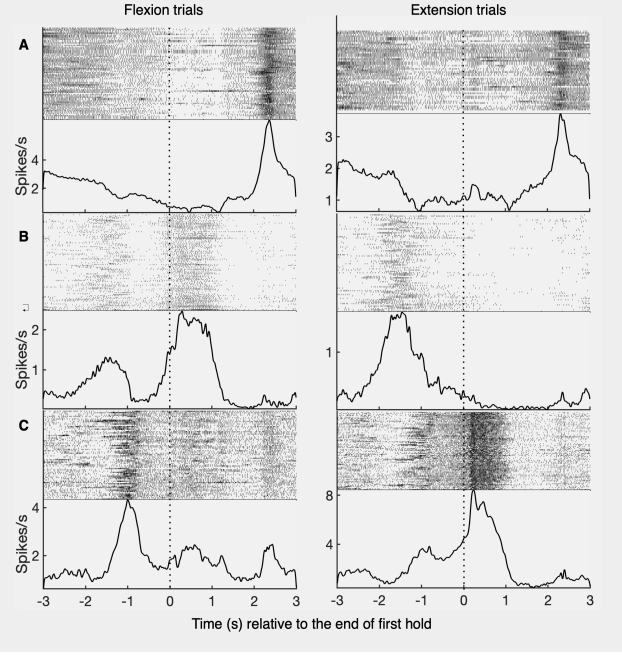
The first part of the analysis looks for evidence for the presence of neural integrator involved in finger movements. For this, four different kinds of movements are taken into account. The second part analyzes how different brain regions encode movement, position, and state during a movement. This is implemented using logistic regression. Also, to see the performance of the neurons in each of these brain regions in encoding position, the neural data were projected on to the first principal component of the neural activity during the second hold period.



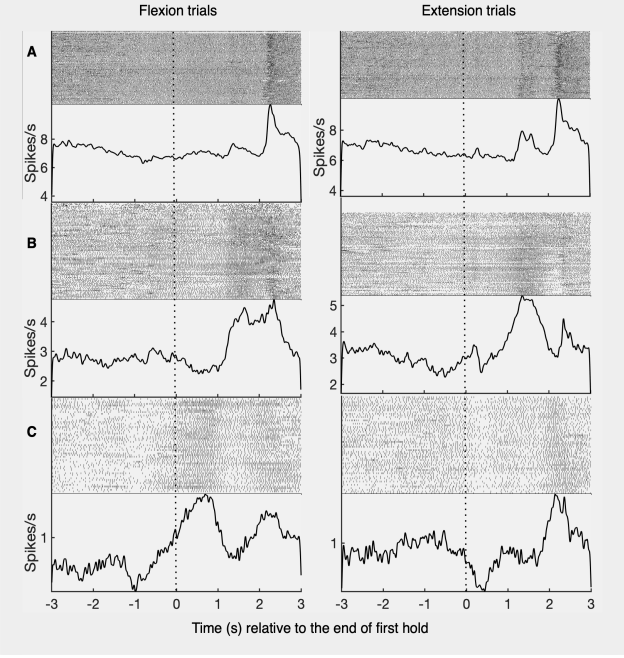
(a) Primary motor cortex



(b) Reticular formation



(c) Spinal cord



(d) Deep cerebellar nuclei

Figure 1.3: Example raster plots and the corresponding peristimulus time histograms of neurons from each brain region

Chapter 2

Neural integrator for finger movements

2.1 Introduction

2.1.1 The neural integrator hypothesis

The neural integrator is one of the important models of short-term memory. The evidence of its presence in the oculomotor system has been corroborated in the previous studies. The concept of the neural integrator is an explanation for how the effect of a stimulus persists for a short period even after the stimulus stops. In the oculomotor system, from the recordings from the motor neurons during eye movements, the activity of the neurons seem to be related to the position of the eye[11]. It is therefore apparent that these neurons encode the position of eye movement. From the recordings of neural activity from the premotor burst neurons, it is conspicuous that the burst neurons encode the velocity, as they are active only when there is movement[10]. The premotor neuron stops firing if there is no velocity input.

But things get complicated when the premotor neurons are stimulated for a short period. When the neuron is stimulated for a short period, this induces a velocity, and brings a concomitant change in position. Let the position of the eye change from x_1 to x_2. Once the stimulation period is over, there is no more velocity induced. Because there is no stimulation in the neurons encoding position, the eye has to go back to its initial position x_1. But this doesn't happen. The

eye remains at x_2 for a short period even after the stimulus to the burst neuron is turned off[3]. The explanation for how the stimulation of the premotor burst neurons lead to gaze holding lies in the concept of the neural integrator.

A possible explanation for this is that as the moving system comprising of the premotor neurons receive input from the eye movement, an efference copy of it is sent to another system in the eye called the neural integrator. This system integrates the velocity and thereby encodes the position information. The prepositus neurons act as a neural integrator for the eye movements[6]. There is evidence suggesting that prepositus in fact encodes position by integrating the movement information, as in one of the previous studies it was observed that the eyes lost the ability to stay still at a position once the prepositus neurons were shut off by injecting neurotoxins[2].

Is there a similar neural integrator involved in the finger movements? It is possible that the reach controller in the cortical region sends a copy of the velocity signal to the reach integrator in the subcortical region, and the final output is sent to the spinal motor system[1]. To corroborate the theory, the analysis required to find the correlation between the muscle activity during the hold period and the integral of the muscle activity in the preceding move period. For a finger movement starting at t_0 and ending at T with a hold muscle activity of $u(h_1)$ prior to the movement onset, and a hold muscle activity of $u(h_2)$ after the end of the movement, the neural integrator hypothesis can be summed up using the equation 2.1.

$$u(h_2) - u(h_1) \approx k \int_{t_0}^{T} [u(\tau) - u(h1)] d\tau + a \tag{2.1}$$

Therefore, the change in hold period activity should be roughly a linear function of the integral of muscle activity during the preceding movement with an integration gain k [1].

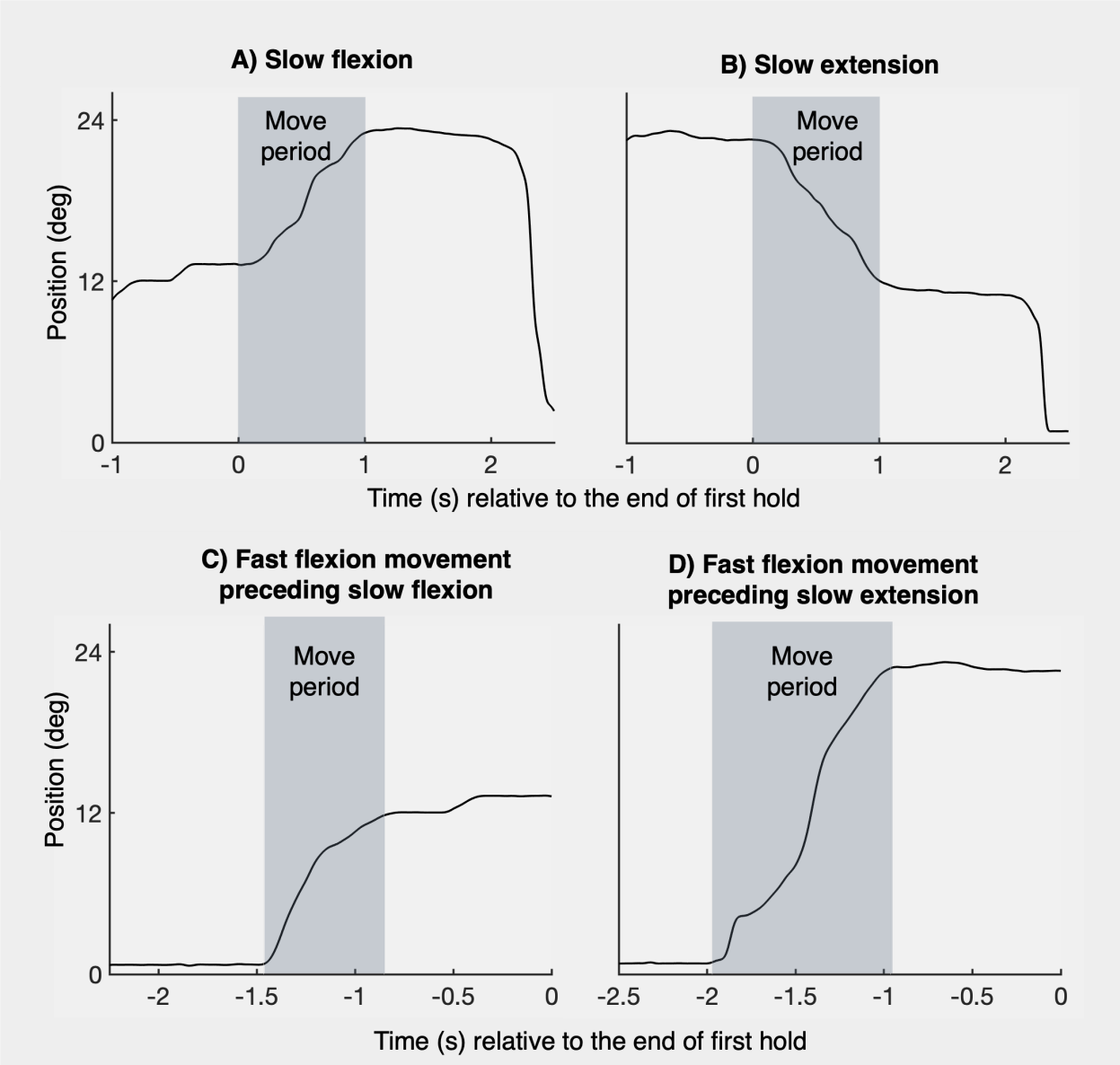


Figure 2.1: The four different types of movements considered for the integrator analysis given in table 2.1

2.1.2 The slow flexion and slow extension movements

These are the movements which the monkeys do voluntarily. Both of these movements start by holding the finger at a position for $1s$, move for $1s$ with a velocity $12^o/s$, and hold the finger once again at the final position for another $1s$. The entire duration for this is $3s$. Note that these

Type of movement	Change in position
A: slow flexion	12^o to 24^o
B: slow extension	24^o to 12^o
C: fast flexion before **A**	0^o to 12^o
D: fast flexion before **B**	0^o to 24^o

Table 2.1: The four different types of movements used for integrator analysis and their corresponding change in position shown in figure 1.1

movements result from the monkey tracing the motion of target on the screen. The movements **A** and **B** from the table 2.1 and the figure 1.1 fall under this category.

2.1.3 The fast flexion movements

These are the involuntary finger movements that result from the monkey adjusting the finger prior to the slow movements. There are two types of fast flexion movements - the fast flexion movement preceding slow flexion movement and the fast flexion movement preceding slow extension movement. These are given by the movements **C** and **D** in figure 1.1 and 2.1. These movements seem to consist of an initial hold period, a move period, and a final hold period, and all of these take place in less than $2.5s$. It is because these movements are faster than the movements **A** and **B** that these movements are referred to as being fast.

2.2 Materials and methods

There were 191 sessions of recordings of the muscle activity and the lever position in total, each with different number of flexion and extension trials.

2.2.1 Finding the movement onset and duration for fast flexion movements

Since the fast flexion movements are not part of the experimental set-up per se, it was imperative to find the movement onset and the duration of movement before applying the neural integrator hypothesis to the fast flexion movement data. It was safe to assume that the monkey adjusts the finger to a particular position (12^o before flexion and 24^o before extension) before attempting a flexion or extension movement of the finger within $1.5s$ before the beginning of the first hold. Therefore, only the lever position data and EMG data within an interval of $2.5s$ before the start of the movement was taken into account for detecting the onset and duration of the fast flexion movements.

However, not all the trials had movement data that were eligible to be considered as flexion movements. In some trials, the monkey had to adjust the finger to only a small extent prior to the experiment. This happens when the finger is not initially at or closer to the equilibrium position, 0^o, but is closer to the required final position by chance. In this case, there is almost no room for a flexion movement to bring the finger to the intended position to start the slow flexion and slow extension movements. In some other cases, although the monkey starts adjusting the finger from a position closer to 0^o, the monkey might flex the finger to a larger extent than intended, and attempts an extension movement to compensate for this extra flexion movement. Although this qualifies as a flexion movement, the extension component of the movement introduces heterogeneity to the position data, making it necessary to eliminate the fast flexion movements with an extension component to them. To eliminate the trials that didn't possess the attributes of a fast flexion movement that eligible for further analyses were eliminated using a speed filter and position filter. The same speed filter was used for detecting the movement onset and duration for the eligible fast flexion movements.

Position filter

Since the hypothesis requires that there be enough hold time before the movement onset to be used for applying the equation 2.1, only those trials where the monkey held the finger below a threshold of 5^o for a period of $300ms$ within the interval $[-2.5s, -1s]$ were taken into consideration for further analysis. This makes sure that only those trials with flexion movements are considered for further analysis. Since holding the finger at the required final position is part of the original experimental set up (this corresponds to the first hold period for the slow movements), a similar window was not used for eliminating the trials based on the final position. The trials after passing through the position filter are subjected to go through the speed filter.

Speed filter

The speed of the movement was computed from the position data. The peak of the speed trace closer to time $0s$ was obtained. Let this peak speed be v_m. The speed v_m occurs during the fast flexion movement. So the next step was to see if a given trial has a speed below a threshold of $5^o/s$ for a duration of $300ms$ prior to movement. Here, any speed value below the threshold is considered to be part of the noise. Therefore, a window sliding from v_m to the left of the speed trace was used to determine if the speed of the trial falls below the threshold for a necessary period of time for the trial to be considered as consisting of an initial hold period. Once the window encounters a point in the speed trace where all the values in the window to the left of the point fall below the speed threshold, that point is noted. The time corresponding to this point is taken as the start of the fast flexion movement.

Similarly, another sliding window of length $300ms$ was used again, this time sliding to the right of the speed trace from v_m. This makes sure that the trial will have the finger positioned at the required final position for a given period of time to be considered to consist of a second hold period. Once the point where all the values of the speed fall below the threshold in the window

to the right of the point is encountered, the point is noted, and the time corresponding to this is taken to be the end of the fast flexion movement.

Figure 2.2 shows one example each for how the position and speed filters are applied for fast flexion preceding slow flexion movement and fast flexion preceding slow extension movement.

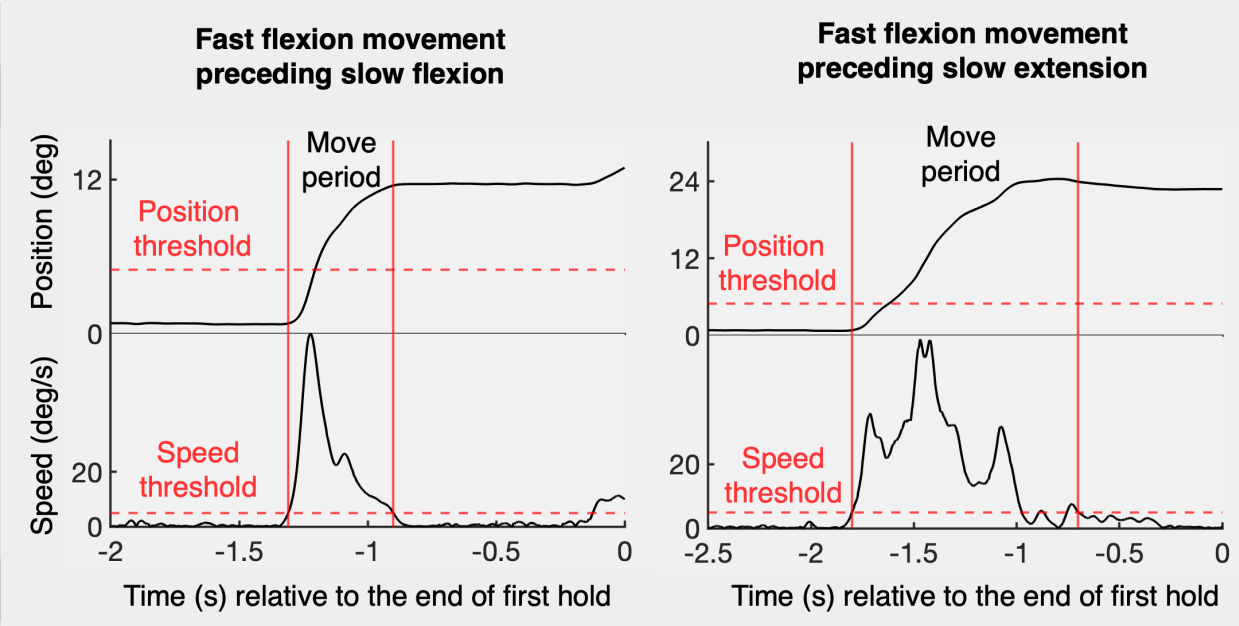


Figure 2.2: The use of position filter and velocity filter in eliminating the outliers and finding the movement onset and duration

2.2.2 Preprocessing the position and EMG data

Before proceeding on to the analysis part, some preprocessing of the EMG and lever position data were required. The sessions in which the EMG data for all the trials seemed to consist mostly of noise were eliminated by visual inspection. For each session, the trials in which the EMG value remained zero throughout were eliminated by setting a threshold to the peak value. There were some trials in some sessions in which the overall muscle activity seemed way higher or lower than most of the trials. These trials were eliminated with the help of median absolute

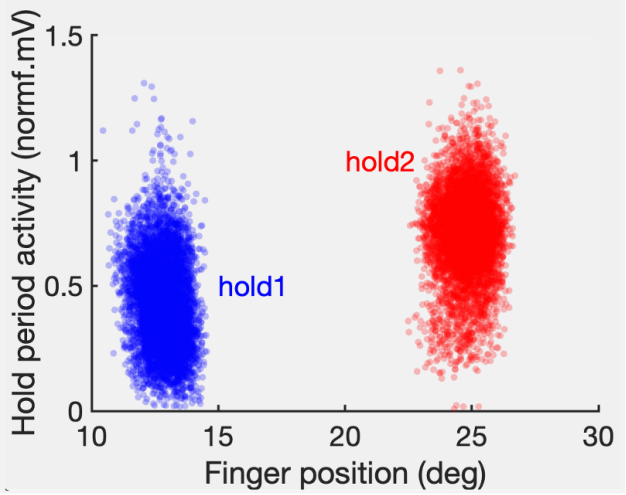
deviation of the peak EMG value of the trials. If the peak value of a trial was not within 3 median absolute deviations from the mean of the peak values, that trial was eliminated. The EMG data were collapsed across all the sessions after normalization. To normalize, the muscle activity was divided by the mean of the peak values of the trials in the session.

2.2.3 The neural integrator hypothesis applied to the four movement types

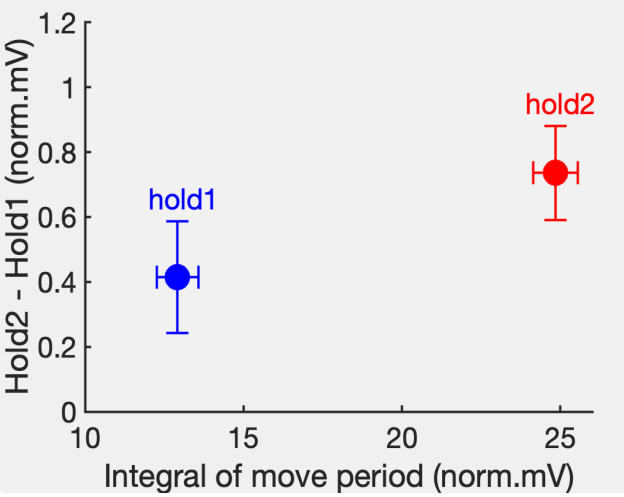
From the equation 2.1, it is conspicuous that to look for evidence of a neural integrator involved in finger movements, three variables are required: $u(h_1)$, which is the mean muscle activity during the first hold, $u(h_2)$, which is the mean muscle activity during the second hold, and the integral of the muscle activity during the move period. The mean of the muscle activity over a $400ms$ interval starting $1s$ prior to movement onset was taken to be $u(h_1)$. This is to eliminate any kind of pre-movement activity that might be present just before the movement onset. $u(h_2)$ was the mean muscle activity over a $200ms$ interval starting $700ms$ after the end of the movement. The integration was done over a $1150ms$ interval starting $150ms$ before the movement onset. The integration was done on all the 9 muscles separately, and also after collapsing the data across all the muscles.

2.3 Results

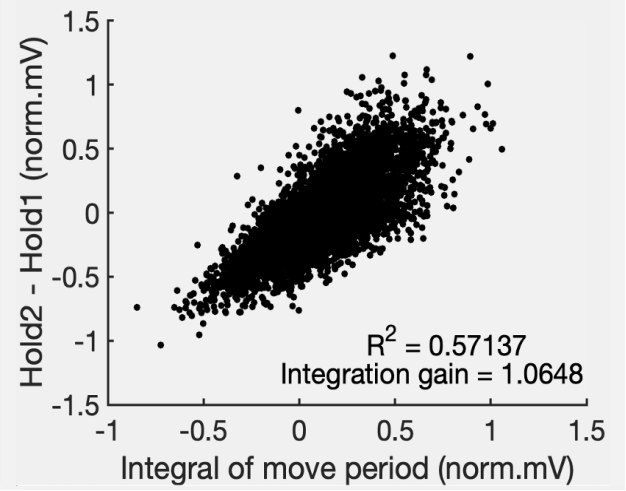
As the figure 2.3 shows, for slow flexion movements where the finger goes from 12^o to 24^o, there is a fairly high correlation between integral of the muscle activity in the move period and the muscle activity in the hold period that follows it for each of the muscles separately, and on combining the data from all the muscles together. For slow extension movements the correlation coefficient is quite high as well as it is conspicuous from figure 2.4d, pointing to the possibility



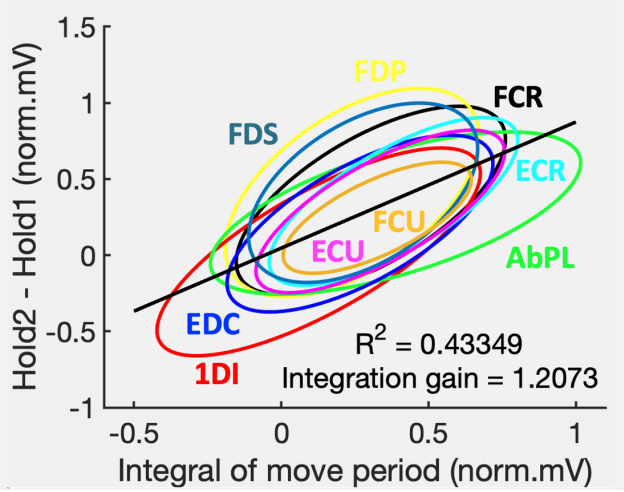
(a) The mean muscle activity during the first hold and second for the muscle ECU for the slow flexion movements



(b) The error bar for the mean muscle activity during the first hold and second for the muscle ECU for the slow flexion movements



(c) Fitting a regression line to see how the integral of the muscle activity in the move period is related to the position of the finger during the hold period for the muscle ECU (n = 6486)

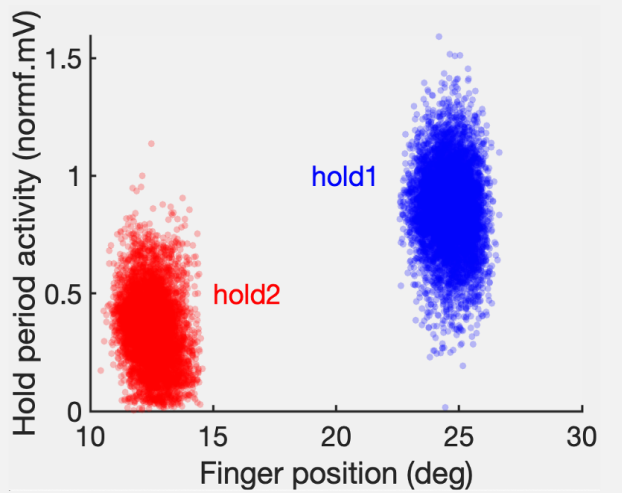


(d) Collapsing the data across all the muscles and analyzing how the integral of the muscle activity in the move period correlates to the position of the finger during the hold period (n = 51852)

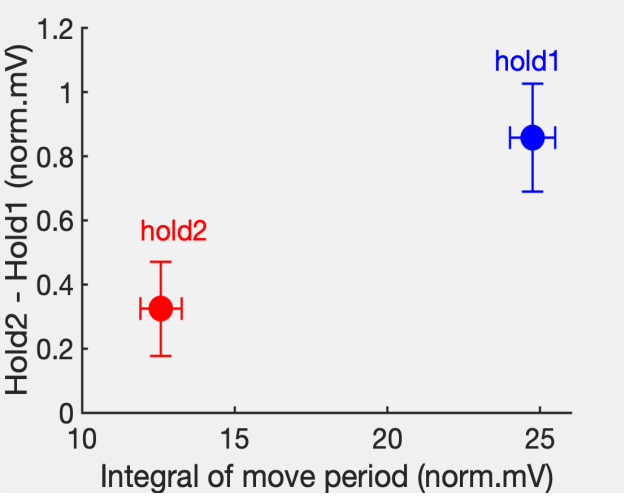
Figure 2.3: Results on testing out the neural integrator hypothesis on the slow flexion movements

of the presence of a neural integrator involved in the voluntary movements.

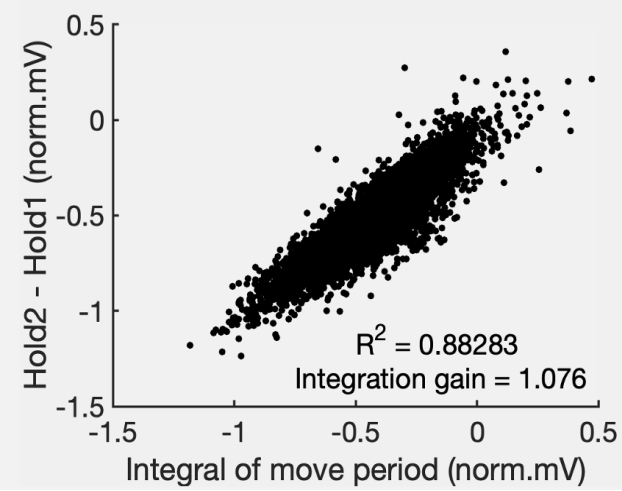
The results on applying neural integrator hypothesis to both of the fast flexion movements, given in figures 2.5d and 2.6d also show high correlation between the muscle activity during hold period and the integral of the muscle activity in the preceding move period. This supports the assumption



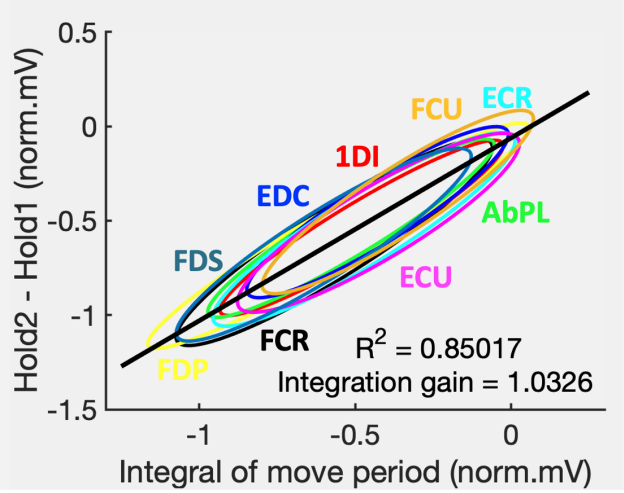
(a) The mean muscle activity during the first hold and second for the muscle ECU for the slow extension movements



(b) The error bar for the mean muscle activity during the first hold and second for the muscle ECU for the slow extension movements



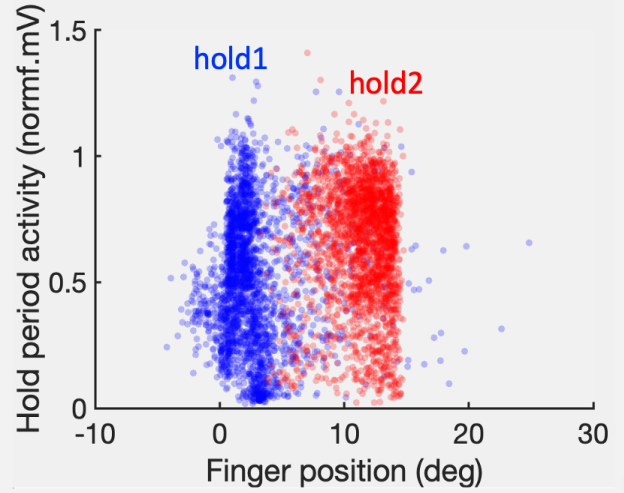
(c) Fitting a regression line to see how the integral of the muscle activity in the move period is related to the position of the finger during the hold period for the muscle ECU (n = 6826)



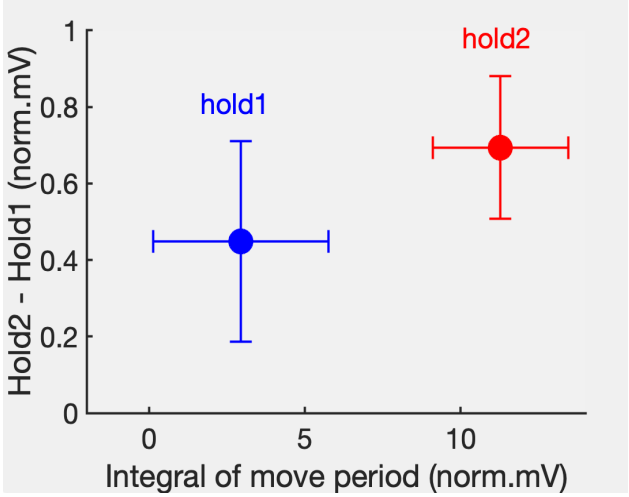
(d) Collapsing the data across all the muscles and analyzing how the integral of the muscle activity in the move period correlates to the position of the finger during the hold period (n = 53544)

Figure 2.4: Results on testing out the neural integrator hypothesis on the slow extension movements

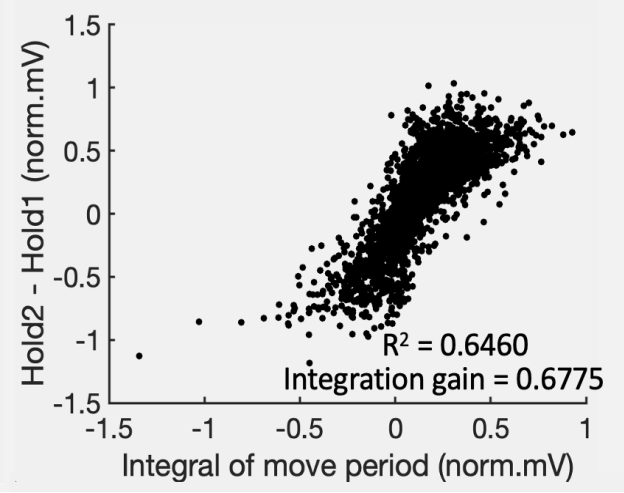
that a neural integrator might be involved in the finger movements regardless of the movement being voluntary or involuntary, slow or fast.



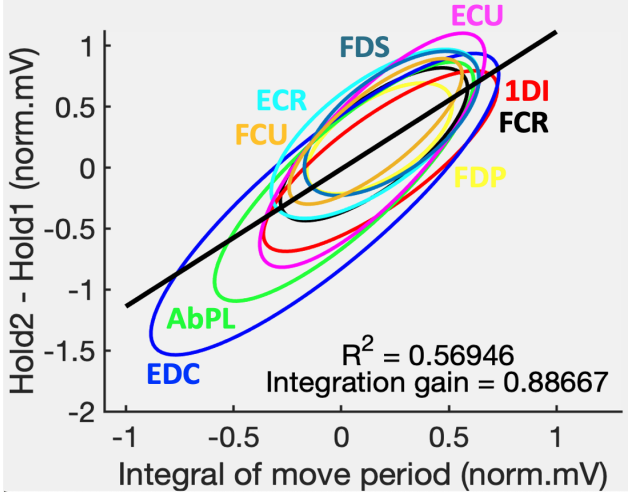
(a) The mean muscle activity during the first hold and second for the muscle ECU for the fast flexion movement preceding the slow flexion movements



(b) The error bar for the mean muscle activity during the first hold and second for ECU for the fast flexion movements preceding slow flexion movements



(c) Fitting a regression line to see how the integral of the muscle activity in the move period is related to the position of the finger during the hold period for the muscle ECU (n = 2527)

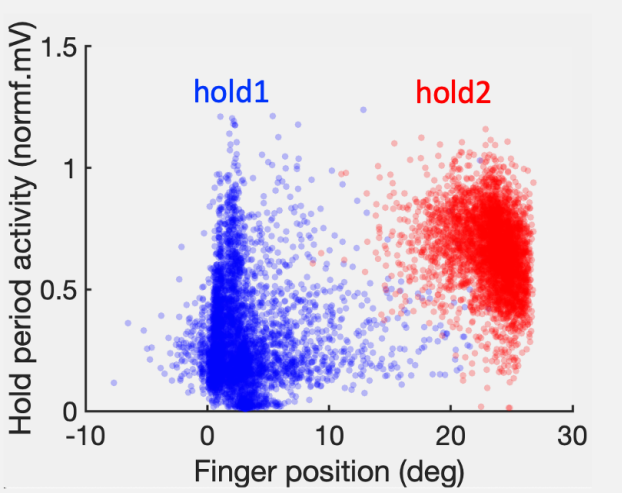


(d) Collapsing the data across all the muscles and analyzing how the integral of the muscle activity in the move period correlates to the position of the finger during the hold period (n = 19399)

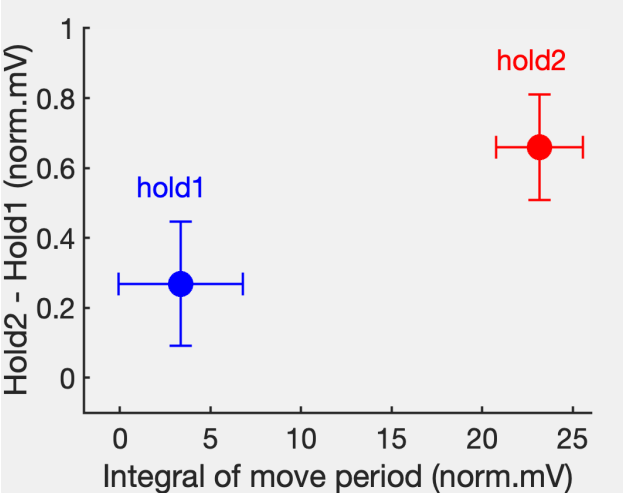
Figure 2.5: Results on testing out the neural integrator hypothesis on the fast flexion movements preceding slow flexion movements

2.4 Discussion

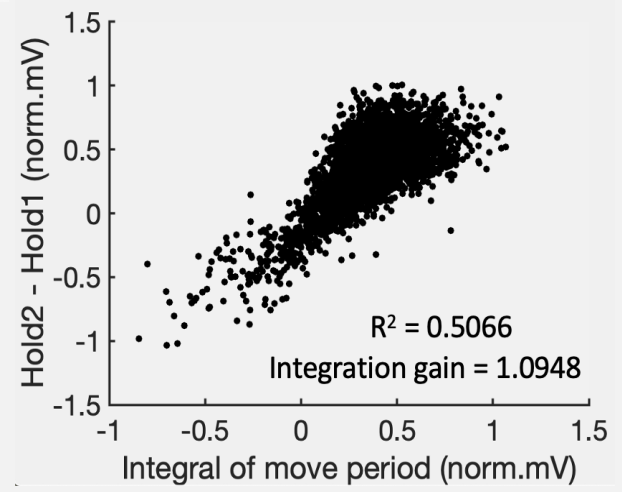
From the results, it is quite apparent that the muscles have higher mean activity as the distance increases. Also, the correlation between the mean muscle activity during the hold period and the



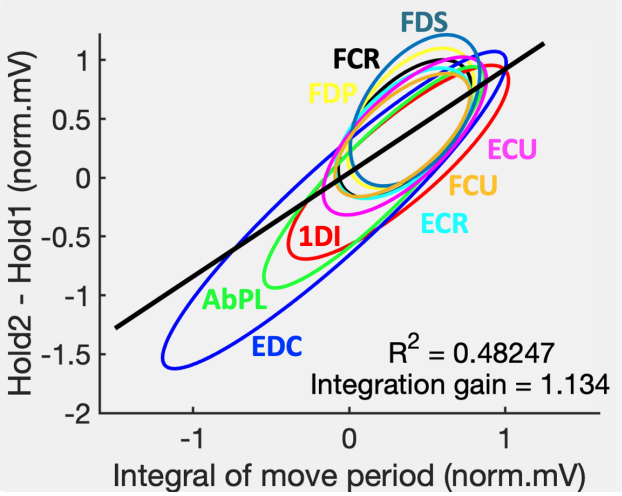
(a) The mean muscle activity during the first hold and second for the muscle ECU for the fast flexion movement preceding the slow extension movements



(b) The error bar for the mean muscle activity during the first hold and second for ECU for the fast flexion movements preceding slow extension movements



(c) Fitting a regression line to see how the integral of the muscle activity in the move period is related to the position of the finger during the hold period for the muscle ECU (n = 4100)



(d) Collapsing the data across all the muscles and analyzing how the integral of the muscle activity in the move period correlates to the position of the finger during the hold period (n = 32704)

Figure 2.6: Results on testing out the neural integrator hypothesis on the fast flexion movements preceding slow extension movements

integral of the muscle activity during the preceding move period seems to be quite high. Such a high correlation is observed regardless of the speed and type of the movements. This points to the possibility that a neural integrator might be involved in finger movements that integrates the

movement command to yield the information for position.

Chapter 3

Neurons encoding state, position, and movement

3.1 Introduction

In this chapter, the neural data from four brain regions - the primary motor cortex, the deep cerebellar nuclei, the spinal cord, and the reticular formation - that contribute to motor control are analyzed. The deep cerebellar nuclei relays all output from the cerebellar cortex to cortical and subcortical targets. This region is involved in exploratory movements and procedural memory such as motor skill acquisition[5]. In addition to awakening the brain to consciousness and keeping it alert the reticular formation tempers and refines our muscular activity and bodily movements[4]. The key function of primary motor cortex is to control voluntary movements. In addition to being a static motor control structure, it also contains a dynamic substrate that participates in motor learning[7]. The spinal cord provides a means of communication between the brain and the peripheral nerves that enter the cord. It also produces reflexes called the spinal reflexes[8]. The main objective of this chapter is to analyze to what extent these different areas contribute towards encoding position, movement, and state.

3.2 Materials and methods

The neural data was used to create the spike time matrices for every neuron. There were 585 neurons in total, and the neural data was recorded from 4 different brain regions - the primary motor cortex, the reticular formation, the spinal cord, and the deep cerebellar nuclei.

To get the time points of the spikes from a neuron, spike time matrices were created for all the neurons. This spike time matrices were used to create a spike bin matrix of bin width $1ms$. A spike bin matrix gives the number of spikes in a given interval within a trial for a neuron. Each of these spike bin matrices were subjected to Gaussian smoothing of $20ms$ window length. The mean of this matrix across all the trials was taken to create a peristimulus time histogram.

3.2.1 Logistic regression to see how different brain regions encode position, state, and velocity

Logistic regression to see how different brain regions encode velocity

Here the objective is essentially to find how good the different brain regions are at classifying the flexion movements from extension movements. Figure 3.6 shows these two different types of movements. Each neuron has different number of trials and logistic regression was applied to each neuron.

For one neuron, its spike bin matrix corresponding to flexion movement was taken, and the data over a $1s$ interval from the movement onset was extracted. The mean neural activity of each trial across this time interval was computed, and labelled as $1's$. Similarly, for the same neuron, the data over a $1s$ interval was extracted from the spike bin matrix corresponding to extension. The mean neural activity of each trial across this interval was computed, and were labelled as $0's$. These two data were concatenated together. For implementing the logistic regression once, the data set was sampled randomly, with 80% of the data being taken for training and the rest

20% used for testing. This was carried out 1000 times, with different sets of data for training and testing for each iteration. The accuracy for each iteration was noted. A 95% confidence interval of the accuracy across all these iterations was used to see how a neuron performs in classifying the two different types of movements. This method was carried out for all the neurons of all the 4 brain regions.

Logistic regression to see how different brain regions encode position

Here the goal was to find how well the neurons in a brain region perform when it comes to classifying the position of the finger, that is, if the finger is at 12^o or 24^o. For this, the data over a $400ms$ interval $1s$ before the flexion movement onset was extracted from the spike bin matrix for flexion and the mean for each trial across this interval was labelled as $1's$. This is neural activity during the first hold period for the flexion movement. The data over a $200ms$ interval $700ms$ after extension movement termination was extracted from the spike bin matrix of extension movement and the mean of each trial across this interval was labelled again as $1's$. This is the neural activity during the second hold period for the extension movement. Both of these correspond to mean neural activity for every trial at position 12^o.

Now, for the mean neural activity for every trial at position 24^o, the mean neural activity across the first hold period of extension movement and the mean neural activity across the second hold period of flexion movement were extracted from the spike bin matrices. The data over a $400ms$ interval $1s$ before the extension movement onset was extracted from the spike bin matrix for extension and the mean for each trial across this interval was labelled as $0's$. This is neural activity during the first hold period for the extension movement. The data over a $200ms$ interval $700ms$ after flexion movement termination was extracted from the spike bin matrix of flexion movement and the mean of each trial across this interval was labelled again as $0's$. This is the neural activity during the second hold period for the flexion movement. Both of these correspond to mean neural activity for every trial at position 24^o.

Similar to the logistic regression for movement classification, all of these data were concatenated together. For implementing the logistic regression once, the data set was sampled randomly, with 80% of the data being taken for training and the rest 20% used for testing. This was carried out 1000 times, with different sets of data for training and testing for each iteration. The accuracy for each iteration was noted. A 95% confidence interval of the accuracy across all these iterations was used to see how a neuron performs in classifying the two different types of movements. This method was carried out for all the neurons in the 4 brain regions.

Logistic regression to see how different brain regions encode state

Analyzing the performance of a brain region in classifying different stated is equivalent to analyzing the performance of the neurons in the brain region in classifying the neural activity between the first hold and the second hold. This gives us an idea on how good a given neuron is at predicting whether the finger is getting ready for a movement or is already done with the movement.
For this, the data over a $400ms$ interval $1s$ before the movement onset for both flexion and extension were extracted from the spike bin matrices corresponding to both flexion and extension. The mean value across this interval for each trial was computed and these were considered to be the samples from group 1. These are the data for the activity during the first hold of the two movements, flexion and extension. The data over a $200ms$ interval 700 ms after the end of the movement for both flexion and extension were extracted form the spike bin matrices corresponding to both flexion and extension. After finding the mean of every trial across this interval, these were labelled as $0's$. All of these data were concatenated together to be used for logistic regression.
Similar to the two previous logistic regressions, for implementing the logistic regression once, the data set was sampled randomly, with 80% of the data being taken for training and the rest 20% used for testing. This was carried out 1000 times, with different sets of data for training and testing for each iteration. The accuracy for each iteration was noted. A 95% confidence interval of the accuracy across all these iterations was used to see how a neuron performs in classifying

the two different types of movements. This method was carried out for all the neurons in the 4 brain regions.

3.2.2 Principal component analysis to see how different brain regions encode position

The peristimulus time histograms for both flexion and extension movements were collapsed across all the neurons after normalizing by subtracting the mean and dividing with the sum of the standard deviation and a fudge factor. The fudge factor is added to obviate the possibility of division be zero in situations where the standard deviation of a peristimulus time histogram of a neuron turns out to be zero. The data over a $200ms$ interval $700ms$ after the end of the movement for flexion and extension were extracted from this matrix of peristimulus time histograms. This is the neural data corresponding to the second hold period. The first principal component of this data was calculated using principal component analysis, with the neurons as the dimensions and the time points as the samples. The entire neural data corresponding to flexion, which is the peristimulus time histograms collapsed across all the neurons after normalization for the flexion movements, from the start of the first hold to the end of the second hold was projected onto this first principal component of the neural activity during the second hold, and the plots of the results were analyzed. Similarly, the entire neural data corresponding extension, which is the peristimulus time histograms collapsed across all the neurons after normalization for the extension movements, from the start of the first hold to the end of the second hold was projected onto this first principal component of the neural activity during the second hold, and the plots of the results were analyzed as well.

3.3 Results

3.3.1 Primary motor cortex

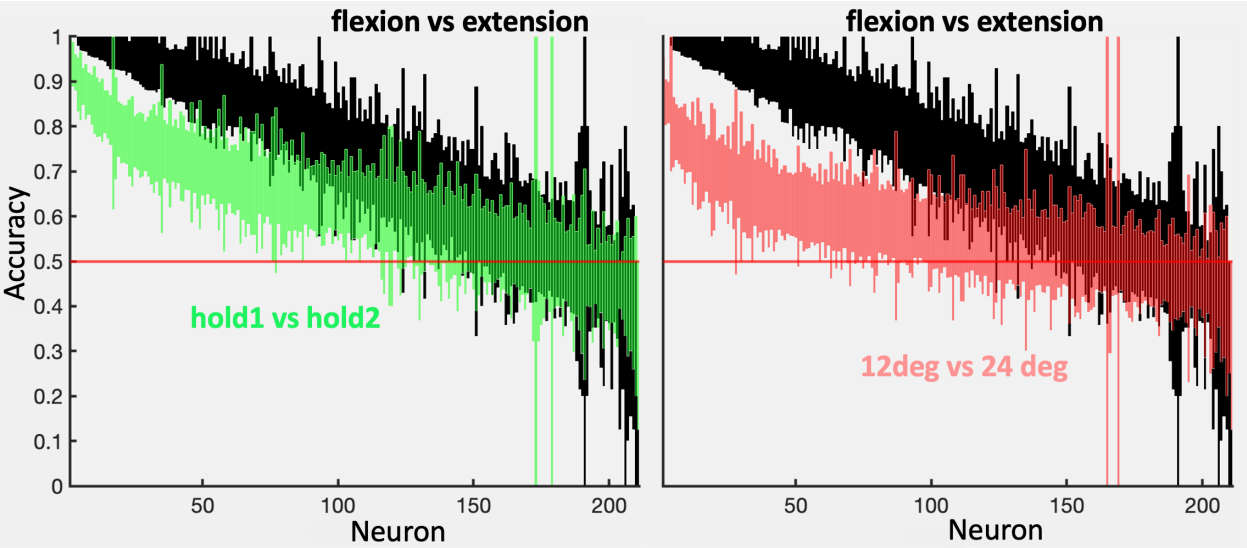


Figure 3.1: Results of logistic regression for the neurons in the primary motor cortex

From figure 3.1, it is evident that the primary motor cortex has more proportion of neurons that encode movement as compared to the proportion of neurons encoding position and state. In addition to this, the accuracy of all the 211 neurons from the primary motor cortex is higher in general when it comes to classifying movements into flexion and extension, as compared to the accuracy for classifying the different positions or states. This points to the possibility that maybe the primary motor cortex is better at encoding movement than it is at encoding position or state. Another noteworthy conclusion is that almost half of the neurons perform better than chance for encoding position and state, and around 70% of the neurons classify the movements better than chance.

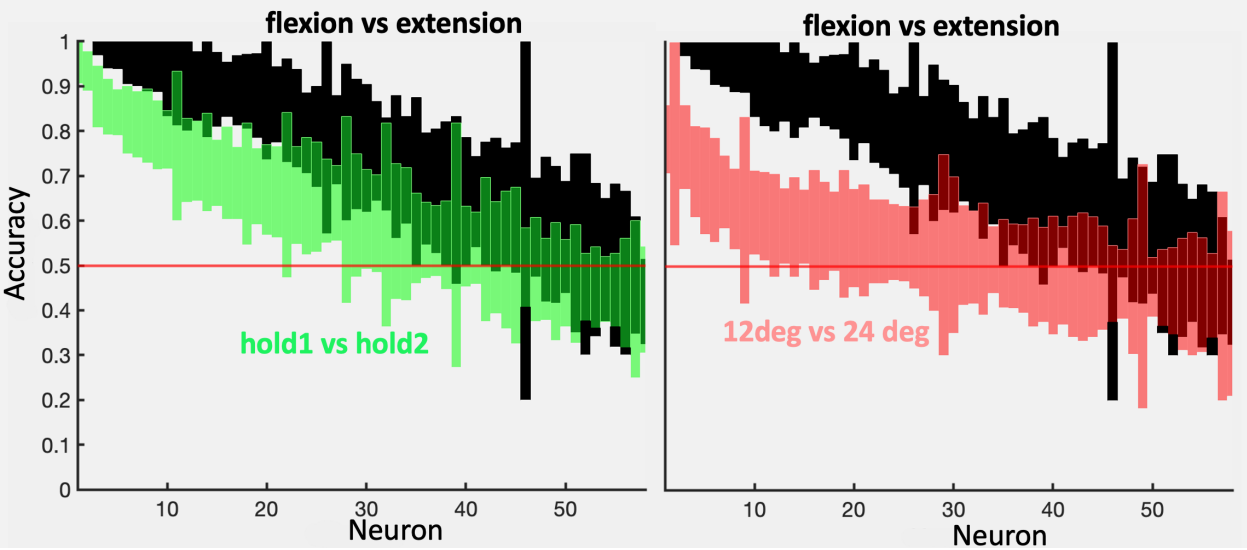


Figure 3.2: Results of logistic regression for the neurons in the reticular formation

3.3.2 Reticular formation

There were recordings from 61 neurons from the reticular formation in total. The results of logistic regression are given by figure 3.2. Here too, the neurons seem to be better at encoding movement as compared to position and state. This is apparent from the fact that the number of neurons with high accuracy of classification is comparatively higher when it comes to classifying movement, and that the accuracy of these neurons for classification of movement is also comparatively higher in general. Therefore, may be the reticular formation does a better job at classifying movement than it does in classifying position and state. Most of the neurons seem to be not performing better than chance when it comes to classifying position, and around 50% of the neurons seem to perform better than chance at encoding state. On the other hand, around 70% of the neurons are better than chance at classifying movements into flexion and extension.

3.3.3 Spinal cord

The results on applying logistic regression to the 119 neurons from the spinal cord are given in figure 3.3. Here, the proportion of neurons that seem to be performing good seems to be almost

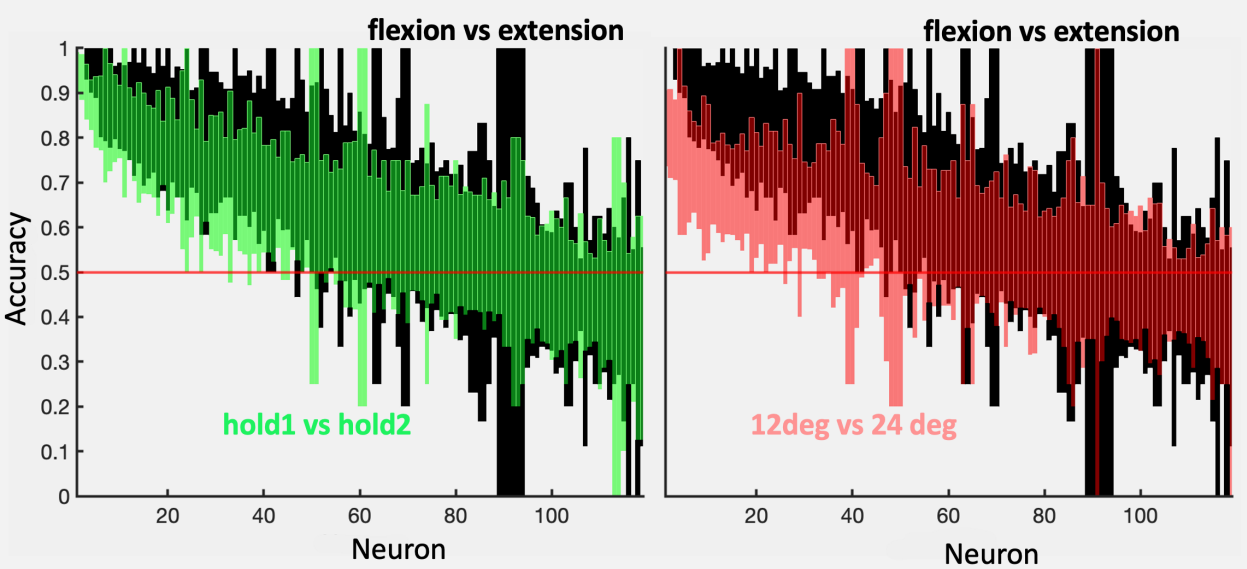


Figure 3.3: Results of logistic regression for the neurons in the spinal cord

equal in all the three scenarios. In all of these three cases, almost half of the neurons seem to be performing better than chance in classifying movements, position, and states. The number of neurons that seem to encode position is lower than the neurons encoding the other two. In addition to this, the accuracy is lower in general when the neurons classify positions.

3.3.4 Deep cerebellar nuclei

The results of carrying out logistic regression to the 69 neurons in the deep cerebellar neuron is given in figure 3.4. Here, the proportion of the neurons performing all the three cases of classification better than chance is less than 50% of the total neurons recorded from the deep cerebellar nuclei. Also, the number of neurons that perform better than chance at classifying positions seems to be lower than the neurons that perform better than chance for the other two classifications. The overall accuracy of the neurons when it comes to classifying positions is also slightly lower as compared to the other two classifications.

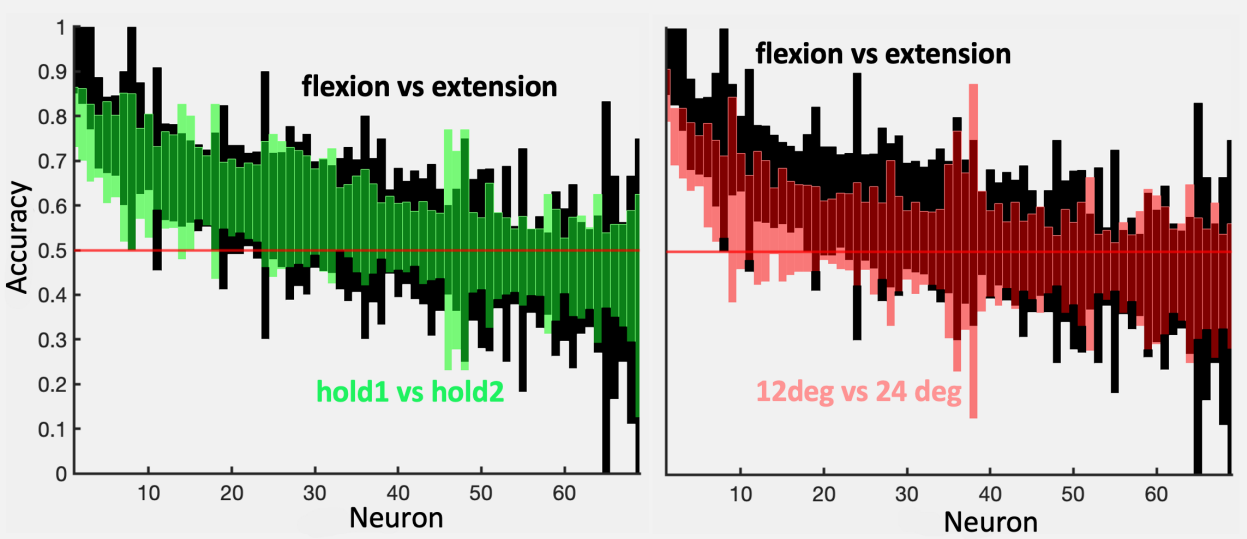


Figure 3.4: Results of logistic regression for the neurons in the deep cerebellar nuclei

3.3.5 Principal component analysis

Since the proportion of neurons that encode position seems to be lower than the neurons encoding movement and state in all the four brain regions, and the performance of the neurons in encoding the position is slightly worse as compared to the performance of the neurons encoding state and movement, principal component analysis was used to see how good these four different brain regions are at encoding position.

The three components of the neural data

The neural data can be thought of as three-dimensional, with one dimension for preparatory activity, one dimension for movement, and a dimension for posture. By projecting the neural data onto each of these dimensions, the performance of the brain regions at encoding these three different components can be evaluated. Fortunately, the true dimension of posture can be obtained by taking the first principal component of the second hold period of movement for both kinds of movements. The reason for not taking the first hold period into consideration here is that the

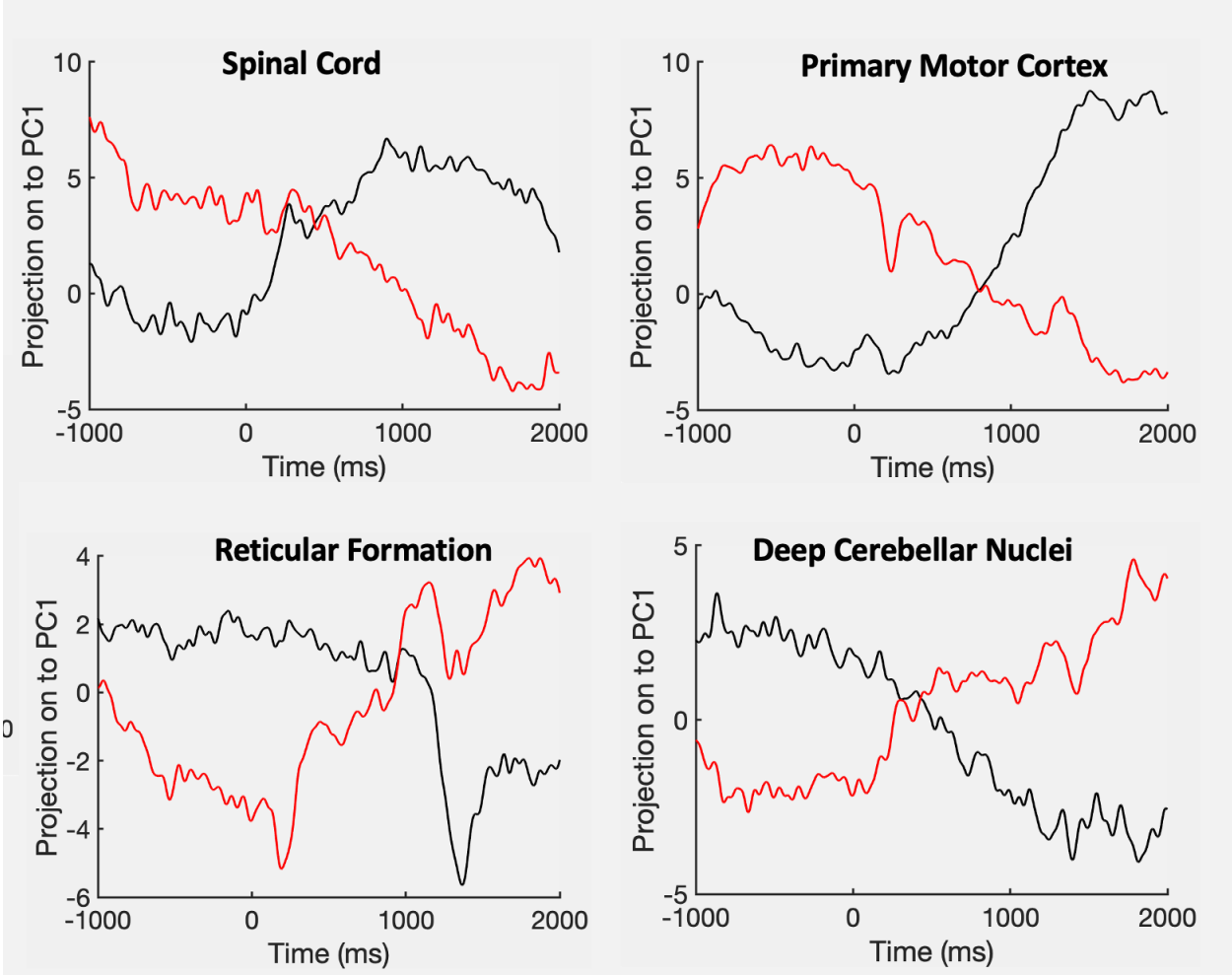


Figure 3.5: Results on projecting the neural data to the first principal component of the neural activity in the second hold period for the different brain regions

first hold period might contain preparatory activity in addition to hold period activity.

Figure 3.5 shows the results on projecting the entire neural data to the first principal component of the activity during the second hold period. These projections seem to reconstruct the position data given in figure 3.6. It is also possible that the spinal cord and primary motor cortex are different in encoding position as compared to reticular formation and deep cerebellar nuclei.

3.4 Discussion

The results of logistic regression point to the possibility of three different types of neurons in all the three regions - those encoding state, position, and movement. The primary motor cortex seems to have a large proportion of neurons encoding movements, and comparatively lower proportion of neurons encoding state and position. This region along with the reticular formation appears to be performing best among all the four regions in encoding movement. For reticular formation as well, the proportion of neurons encoding movement is higher compared to the neurons encoding position and state.

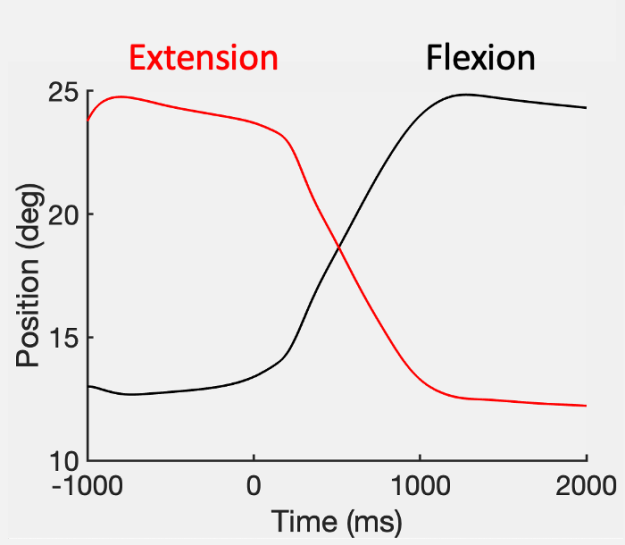


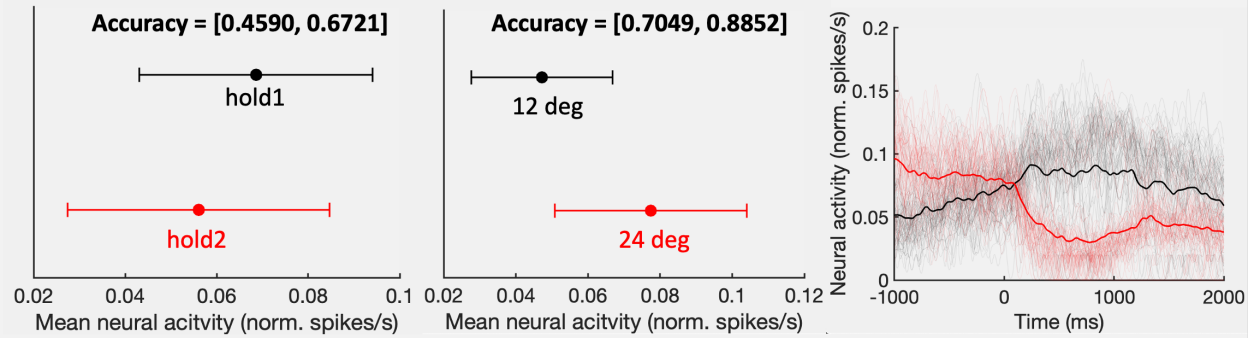
Figure 3.6: The position trace for flexion and extension movements

The spinal cord has similar proportion of neurons encoding position, state, and movement. While the deep cerebellar nuclei also has similar proportions of neurons encoding position, state, and movement, these proportions are lower compared to the other regions.

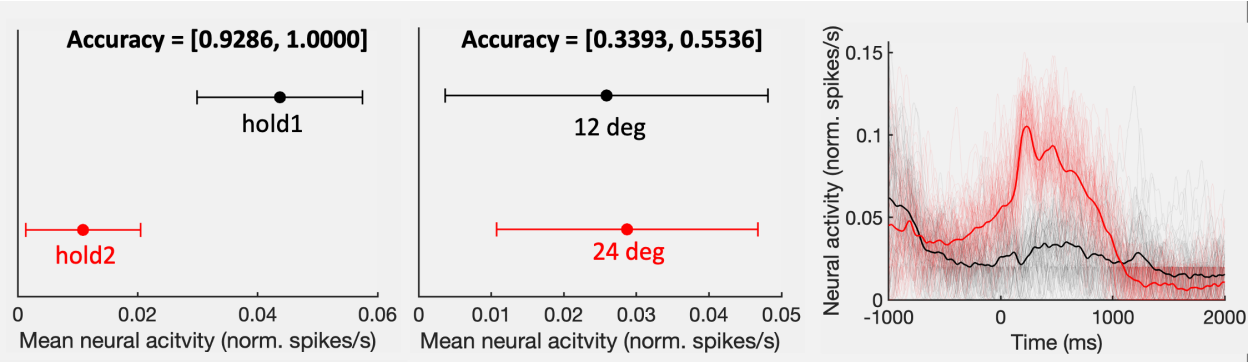
Another noteworthy fact is that a neuron encoding position can not encode state simultaneously. This is due to the way the data were sampled for logistic regression. The figure 3.7a shows the neural activity of the neuron that encodes position. A closer look at the figure shows that the neural activity resembles the position data to some extent. There is also a clear separation between the mean neural activity at 12^o and 24^o. On the other hand, there is no clear separation between the data points corresponding to the first hold period and second hold period. As a result, the accuracy of the neuron is higher in classifying position and lower in classifying state here. Figure 3.7b shows an example neuron encoding state. Here, we see a clear separation of

the data points when for those belonging to the first hold and the second hold, and hence a higher accuracy in classifying the states. There is no clear separation between the data points corresponding to 12^o and 24^o here, resulting in a lower accuracy in classifying positions. While there were neurons that didn't perform well in classifying both position and state, there were no neurons that performed well in encoding both position and state.

Although the proportions of neurons that encode position are lower in all the four brain regions compared to the proportions of neurons encoding the state and movement, all the brain regions still contribute a lot towards encoding position, as it is apparent from the results of principal component analysis. The fact that for all these brain regions, the projection of the neural activity to the position dimension of the neural data recreates the structure of the position data tells that these regions play a major role in encoding position.



(a) Results of logistic regression of a neuron that encodes position with a 95% confidence interval of the accuracy - note that the separation of data for the two positions is quite apparent and the separation of the data for the two states is rather vague (the thicker red trace in the plot for position corresponds to mean of all the neural activity during extension movements and the thicker black trace corresponds to the mean of the neural activity during flexion movements - the thinner lines are the neural activities for each neuron)



(b) Results of logistic regression of a neuron encoding state with a 95% confidence interval of the accuracy - note that there is a clear separation of neural data for the two different states, while the separation of the neural data for two different positions is vague (again, the thicker red trace in the plot for position corresponds to mean of all the neural activity during extension movements and the thicker black trace corresponds to the mean of the neural activity during flexion movements - the thinner lines are the neural activities for each neuron)

Figure 3.7: Two example neurons showing why a neuron can not encode both position and state at the same time

Bibliography

[1] S. T. Albert, A. M. Hadjiosif, J. Jang, A. J. Zimnik, D. S. Soteropoulos, S. N. Baker, M. M. Churchland, J. W. Krakauer, and R. Shadmehr. Postural control of arm and fingers through integration of movement commands. *Elife*, 9:e52507, 2020.

[2] S. Cannon and D. Robinson. Loss of the neural integrator of the oculomotor system from brain stem lesions in monkey. *Journal of neurophysiology*, 57(5):1383–1409, 1987.

[3] B. Cohen and A. Komatsuzaki. Eye movements induced by stimulation of the pontine reticular formation: evidence for integration in oculomotor pathways. *Experimental neurology*, 36(1):101–117, 1972.

[4] J. D. French. The reticular formation. *Scientific American*, 196(5):54–61, 1957.

[5] C. Habas. Functional imaging of the deep cerebellar nuclei: a review. *The Cerebellum*, 9(1):22–28, 2010.

[6] D. A. Robinson. Integrating with neurons. *Annual review of neuroscience*, 12(1):33–45, 1989.

[7] J. N. Sanes and J. P. Donoghue. Plasticity and primary motor cortex. *Annual review of neuroscience*, 23(1):393–415, 2000.

[8] N. A. Silva, N. Sousa, R. L. Reis, and A. J. Salgado. From basics to clinical: a comprehensive review on spinal cord injury. *Progress in neurobiology*, 114:25–57, 2014.

[9] D. S. Soteropoulos, E. R. Williams, and S. N. Baker. Cells in the monkey ponto-medullary reticular formation modulate their activity with slow finger movements. *The Journal of physiology*, 590(16):4011–4027, 2012.

[10] A. Strassman, S. Highstein, and R. McCrea. Anatomy and physiology of saccadic burst neurons in the alert squirrel monkey. i. excitatory burst neurons. *Journal of Comparative Neurology*, 249(3):337–357, 1986.

[11] P. A. Sylvestre and K. E. Cullen. Quantitative analysis of abducens neuron discharge dynamics during saccadic and slow eye movements. *Journal of neurophysiology*, 82(5):2612–2632, 1999.